

## The Larval Stages of Three Pagurid Crabs (Crustacea: Anomura: Paguridae) from Hokkaido, Japan

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**ABSTRACT**—Complementary descriptions of laboratory-reared larvae are given for three hermit crabs from Hokkaido: *Pagurus middendorffii* Brandt, *P. geminus* McLaughlin, and *P. lanuginosus* De Haan. Larval characters of the present material were compared with those of the previous works and some differences were apparent. Morphological evidences suggest that Kurata's zoea II-IV stages of *P. middendorffii* reconstructed from plankton samples should be assigned to another allied species. The number of telsonal processes was constant (=7) in all zoeal stages of both *P. middendorffii* and *P. lanuginosus*.

### INTRODUCTION

The family Paguridae of Hokkaido, northern Japan, contains approximately 15 species [1, 2], and the following four species are predominant in the anomuran population of the seashore in this area: *P. lanuginosus* De Haan, 1849, *Pagurus middendorffii* Brandt, 1851, *P. brachiomastus* (Thallwitz, 1892) and *P. geminus* McLaughlin, 1976. Although the larval stages of these four hermit crabs have been documented [3-6], knowledge on their larvae, however, remains incomplete. Kurata [3] reported four zoeal stages of *P. middendorffii*, reconstructed mainly from the plankton; the magalopa and early crab stages of this species are still unknown. Later he [4] also described the larval development of *P. geminus* (as *P. samuelis* (Stimpson)) reared in the laboratory, but information on several important larval characters, e.g. setation of maxillule, maxilla, and maxillipedal endopods was not given. The larvae of *P. lanuginosus* described from Korean waters [5], and those of our material show two unique features, i.e. constant number of telsonal processes and absence of mandibular palp throughout zoeal stages.

This paper provides: 1) a re-description of zoeal stages and the first descriptions of post-larvae of *P. middendorffii*, 2) complementary information on zoeal stages of *P. geminus* and *P. lanuginosus*, and 3) comparisons of larval characters between the present study and the previous works.

### MATERIALS AND METHODS

The localities and the date of collection of ovigerous females, as well as the date of hatching of zoeas in each species are as follows: *P. middendorffii* (Muroan, Pacific coast, 6 May 1985; hatch out: 13 May 1985; Higashi-Shizunai, Pacific coast, 17 May 1984; hatch out: 21 May 1984), *P. geminus* (Oshoro, Sea of Japan, 20 July 1984; hatch out: 31 July 1984), and *P. lanuginosus* (Usujiri, Pacific coast, 8 May 1985; hatch out: 22 June 1985).

The methods for larval culture, dissection, drawings of the specimens and expression of setal arrangement were almost the same as in previous papers [6, 7] except slight modifications. The carapace length (= CL) of zoeas was measured from the tip of the rostral spine to the posterior margin of the carapace, laterally, and that of megalopas and first crabs (*P. middendorffii*) dorsally from the rostrum to mid-posterior point of the carapace. The present descriptions are pri-

mary based on notes made at the time of observation of the larval and postlarval appendages, and further, supplemented with figures prepared.

## RESULTS

### *Rearing data*

The megalopa of *P. middendorffii* was attained 24–26 days after hatching and the first crab appeared after 32–34 days [7].

Approximately 130 zoea I larvae of *P. lanuginosus* were reared and checked daily for alive, dead larvae and their exuviae in the laboratory. Duration of each larval stage was 4 to 5 days for stages I–III, and 6 to 7 days for stage IV. The zoea II appeared after 6 days of culture, zoea III after 10 days, zoea IV after 14 days, and megalopa after 21 days. Due to a lack of food during 1.5 days (15th–16th days), high mortality of zoeas III and IV was produced; it is probable that the megalopal stage is attained one or two days before. After 24 days, when most of larvae were in megalopal stage, 3 larvae of zoea IV remained without moulting, probably due to the lack of food. Rearing experiment was terminated 24 days after hatching, obtaining 25 megalopas of which 13 were fixed.

Only zoea I larvae of *P. geminus* were obtained from a single ovigerous female and no attempts were made to obtain the following stages.

### *Descriptions of larval stages*

#### *Pagurus middendorffii* Brandt, 1851

##### *First Zoea*

Dimension: CL=1.31–1.36 mm (mean 1.34 mm).

Carapace (Fig. 1A): Surface smooth. Rostral spine slightly directed downward, reaching well beyond the antennule and antennal exopod. Posterolateral spines short. Eyes sessile.

Antennule (Fig. 2A): Peduncle unsegmented, elongate, with 2 aesthetascs and 3 setules distally, and a subterminal, long plumose seta projecting beyond the aesthetascs.

Antenna (Fig. 2G, g): Biramous; endopod fused with peduncle, pointed distally, slightly shorter than the exopod (=scale). The latter distally projected as a stout spine, fringed with 5 long plumose setae and a distal shorter simple seta. A stout serrate spine emerging proximally near base of endopod.

Mandible (Fig. 3A): Both asymmetrical, slightly different in dentition. Incisor process stout, rather short. Molar process with several pointed teeth of different lengths and minute granules on inner surface.

Maxillule (Fig. 3G): Endopod 3-segmented, with setae arranged as 1, 1, 3 of which the proximal seta is very short. Basial<sup>1</sup> endite with 2 large stout spines, each spinulate distally, and 2 fine setae. Coxal endite single-lobed, with 5 plumose and 2 fine setae.

Maxilla (Fig. 4A): Endopod medially stepped, with 6 setae arranged into two groups as 2+4. Basial and coxal endites bilobed, with 5+4 and 5+4 setae respectively. Scaphognathite fringed with 5 soft plumose setae.

Maxilliped 1 (Fig. 5A): Endopod 5-segmented, with setae arranged as 3, 2, 1, 2, 4+I (I=dorsal plumose seta); segments 1–3 with 5–6, 8–10, and 6–8 setules on outer margin respectively. Exopod with 4 long natatory setae. Basis with 9 setae on inner margin.

Maxilliped 2 (Fig. 5G): Endopod 4-segmented, with 2 setae on segments 1–3 and 5 setae on distal segment of which one is dorsal. Five to six fine setules on dorsal margin of the segments 2–3. Exopod with 4 long natatory setae. Basis with 3 setae on inner margin, the distal setae very similar to those of segments 1–3.

Maxilliped 3 (Fig. 5L): Rudimentary, uniramous, unarmed.

Pereiopods (Fig. 1A): Rudimentary, visible laterally beneath the carapace.

Abdomen (Fig. 6A): Composed of 5 segments

<sup>1</sup> In a previous paper [8], Dr. R. W. Ingle (British Museum, Natural History, London, U.K.) has pointed out to one of us (R.Q.) that the adjective *basial* is preferable to "*basal*" as usually has been used, since *basial* is derived from *basis* whereas "*basal*" means "at the base of", and certainly is not specific in this sense.

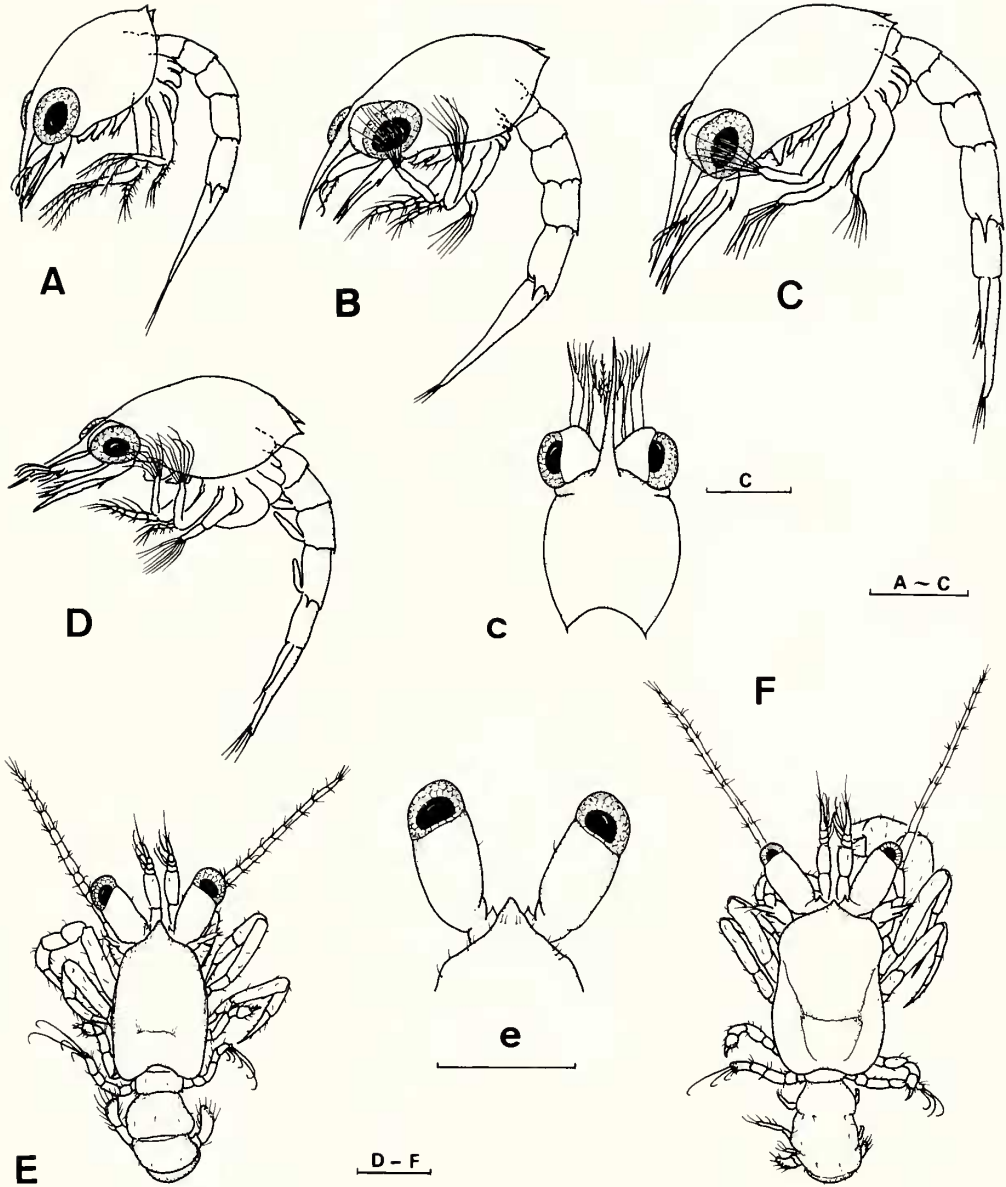


FIG. 1. *Pagurus middendorffii* Brandt, 1851. Whole specimens of zoeal stages I-IV (A-D), lateral view, megalopa (E) and first crab (F), dorsal view; c, zoea III, carapace in dorsal view; e, megalopa, anterior portion of carapace. Scale bars=0.5 mm.

and a telson. Posterior margin of each segment except the first, with 4-5 minute spines; segment 5 with well-developed acute posterolateral spines.

Telson (Fig. 6A): Elongate, posterior margin slightly convex, with 7+7 processes; outermost process a short stout spine, articulated at its base,

the second an inconspicuous fine seta, and the third to seventh are large setae, each finely setulose along margins. Anal spine present medio-ventrally.

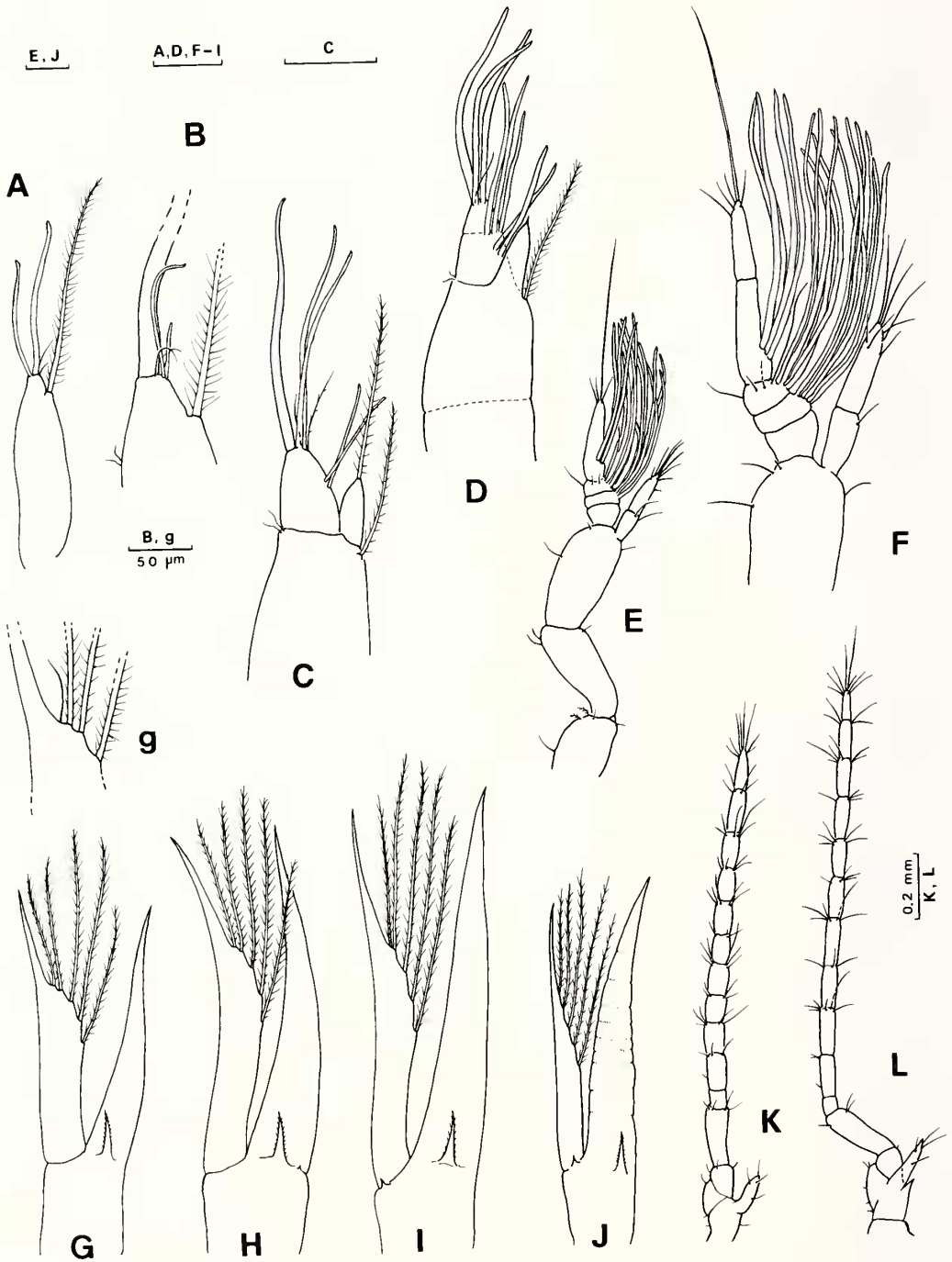


FIG. 2. *Pagurus middendorffii* Brandt, 1851. Antennules and antennae. A-F, antennule of zoea I-IV (A-D), megalopa (E) and first crab (F); G-L, antenna of zoea I-IV (G-J), megalopa (K) and first crab (L); g, detail of apical setae of antennal exopod of zoea I. Scale bars=0.1 mm, except for 50  $\mu$ m (B, g) and 0.2 mm (K, L).

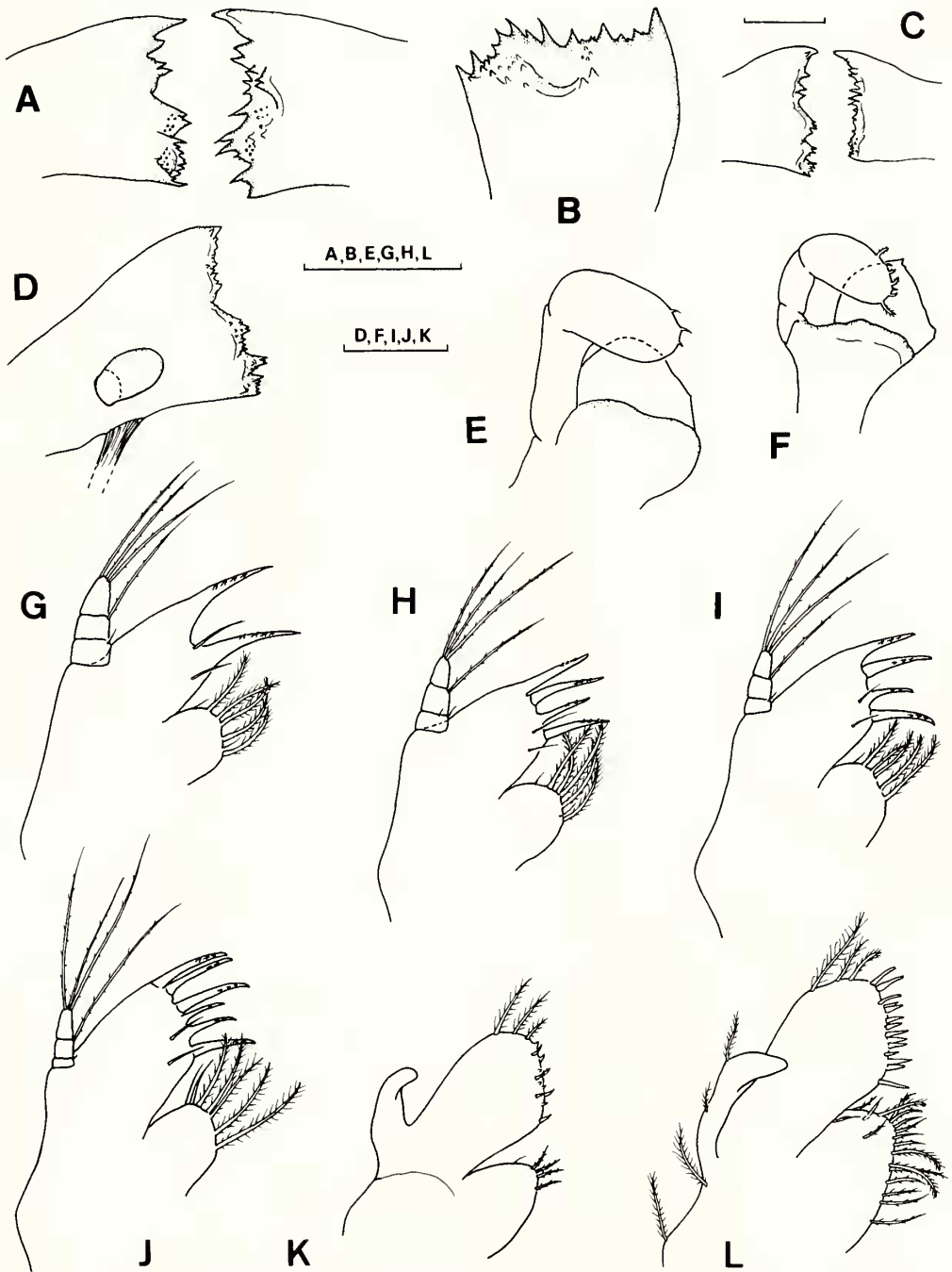


FIG. 3. *Pagurus middendorffii* Brandt, 1851. Mandibles and maxillules. A-F, mandibles of zoea I-IV (A-D), megalopa (E) and first crab (F); G-L, maxillule of zoea I-IV (G-J), megalopa (K) and first crab (L). Scale bars=0.1 mm.



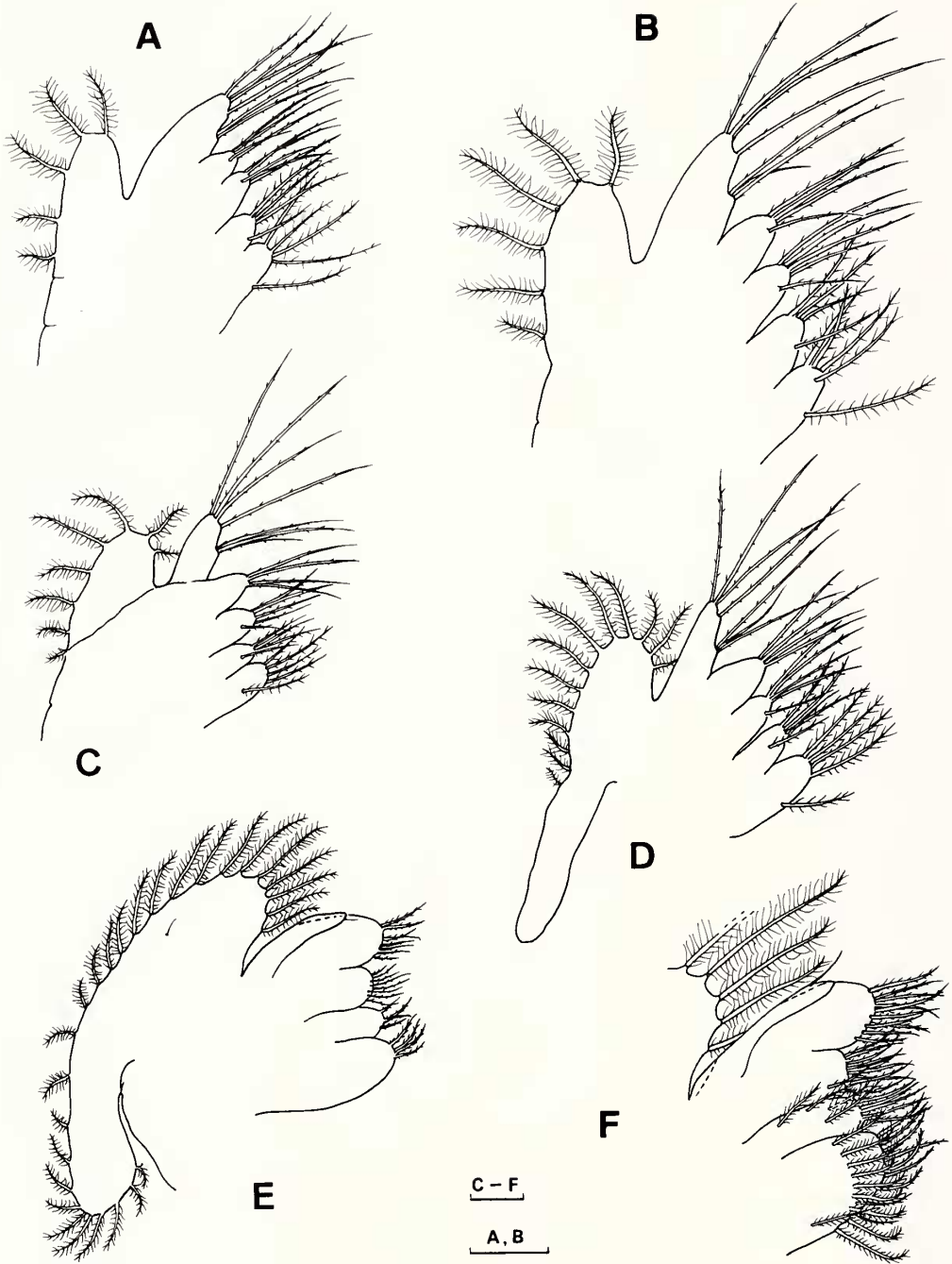


FIG. 4. *Pagurus middendorffii* Brandt, 1851. Maxilla of zoea I-IV (A-D), megalopa (E) and first crab (F). In F, scaphognathite partially drawn. Scale bars = 50  $\mu$ m.

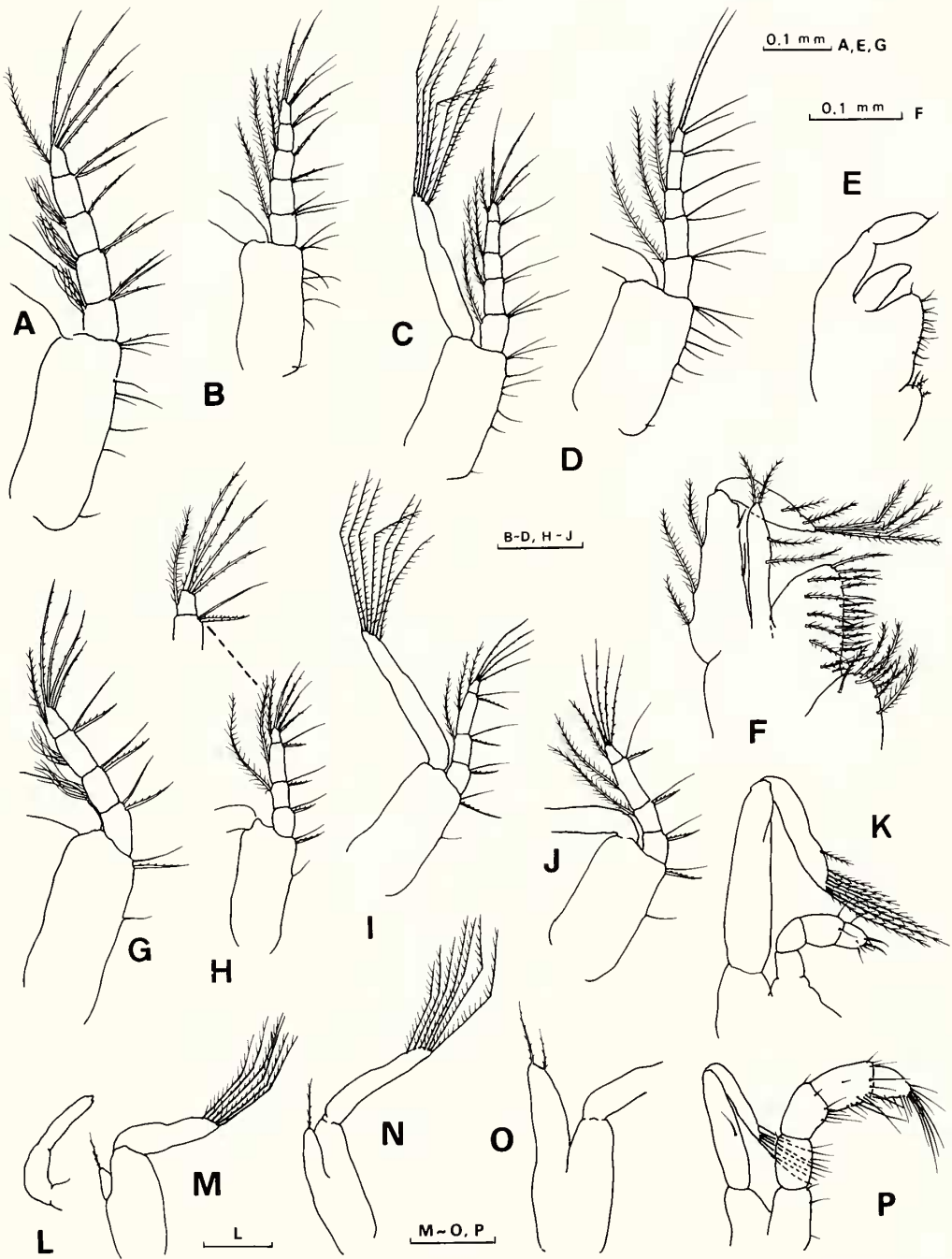


FIG. 5. *Pagurus middendorffii* Brandt, 1851. Maxillipeds. A-F, maxilliped 1 of zoea I-IV (A-D), megalopa (E) and first crab (F); G-K, maxilliped 2 of zoea I-IV (G-J) and of megalopa (K); L-P, maxilliped 3 of zoea I-IV (L-O) and of megalopa (P). Scale bars=0.2 mm, except for 0.1 mm.

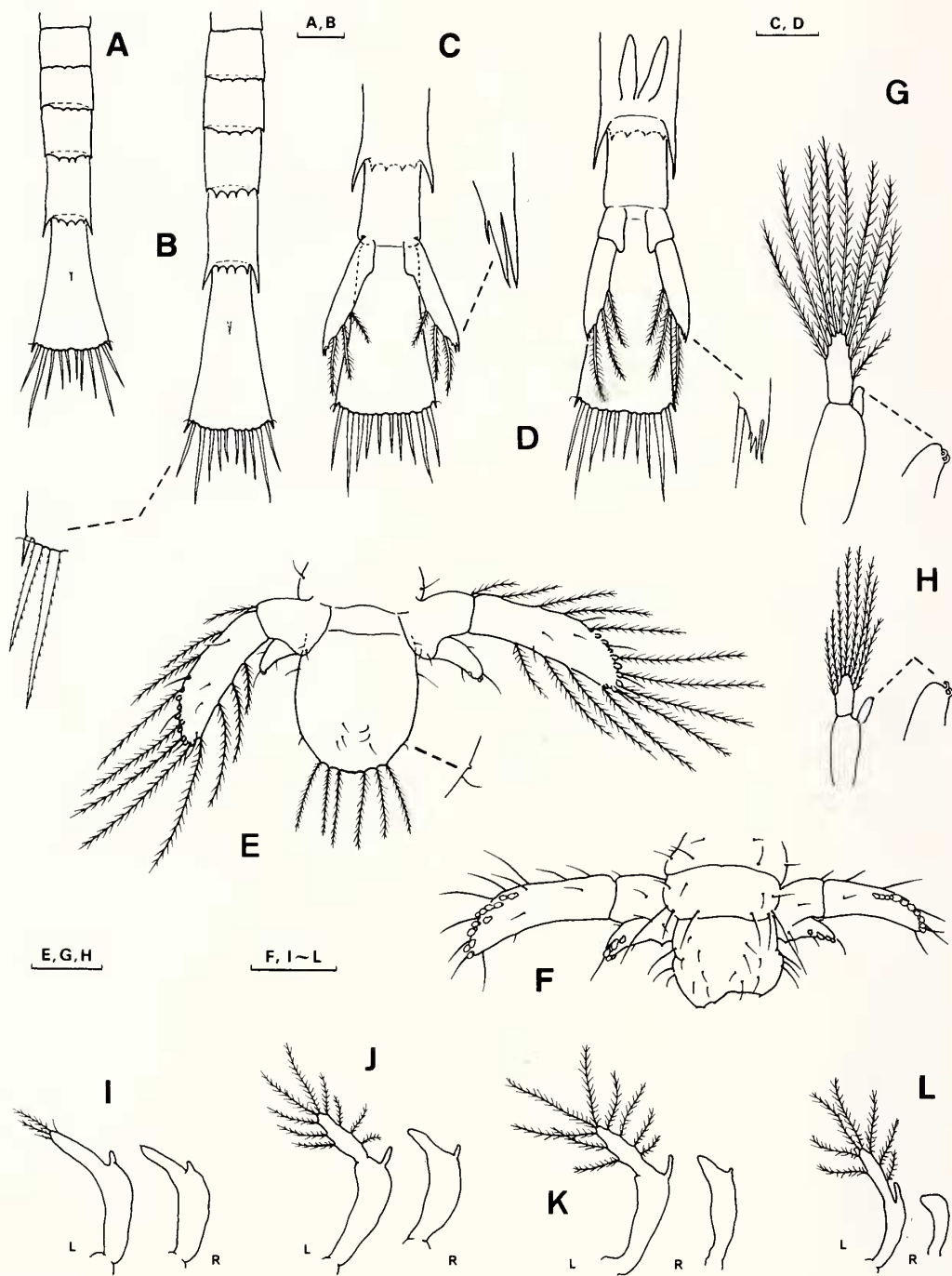


FIG. 6. *Pagurus middendorffii* Brandt, 1851. Abdomens and pleopods. A-D, abdomen and telson of zoeal stages I-IV; E, F, tail fan of megalopa (in ventral view) and of first crab (in dorsal view) respectively; pleopod 1 (G) and 4 (=last) (H) of the megalopa, each with a detail of distal hooked setae on endopod; I-L, pleopods 1-4 of the first crab (R= right pleopod; L= left pleopod). Scale bars=0.2 mm.



*Second Zoea*

Dimension: CL=1.48–1.54 mm (mean 1.51 mm).

Carapace (Fig. 1B): General morphology as in the previous stage. Eyes stalked.

Antennule (Fig. 2B): With 3 aesthetascs and 2 fine setae distally; the two shorter aesthetascs extremely fine, approximately 1/5 of the thick aesthetasc. Subterminal plumose seta not reaching the tip of the longest aesthetasc. Two fine setules on the opposite margin.

Antenna (Fig. 2H): Endopod as long as the exopod. Exopod with 5 plumose setae.

Mandible (Fig. 3B): Longer, but similar in dentition to the previous stage.

Maxillule (Fig. 3H): Endopod with 2, 1, 3 setae; basal two setae hardly observable, but some specimens showed only one minute seta. Basial endite with 4 spinulose stout spines (two articulated at their bases) and 2 fine setae. Coxal endite with 5 plumose and 2 minute setae.

Maxilla (Fig. 4B): Endopod stepped, with 3 (occasionally 2) medial, 1 subterminal and 3 terminal setae. Scaphognathite with 6 soft, plumose setae. The others unchanged.

Maxilliped 1 (Fig. 5B): Endopod 5-segmented, setation as 3, 2, 1, 2, 4, on the inner margin, plus 1 additional long plumose seta on the outer margin of all segments except the fourth one. Exopod with 7 natatory setae. Basis with 9 setae.

Maxilliped 2 (Fig. 5H): Endopod 4-segmented, setation as 2, 2, 2, 4 (rarely 3) on inner margin, plus additional long plumose seta on the outer margin of segments 2–4. Exopod with 7 natatory plumose setae. Basis with 3 setae.

Maxilliped 3 (Fig. 5M): Endopod vestigial, with a single seta apically. Exopod with 6 plumose setae.

Pereiopods (Fig. 7A): As rudimentary buds, unsegmented; first pereiopod broader, non-chelate.

Abdomen (Fig. 6B): Minute posterolateral spines on segments 2–4, well-developed spines on the segment 5. The others unchanged.

Telson (Fig. 6B): General morphology unchanged.

*Third Zoea*

Dimension: CL=1.74–1.86 mm (mean 1.82 mm).

Carapace (Fig. 1C): Larger, but similar to the previous stages in general morphology.

Antennule (Fig. 2C): Exopod with 3 subequal terminal aesthetascs and 2 additional medial aesthetascs. Endopod well developed, with 1 apical long plumose seta. Another similar seta near base of endopod, and 2 minute setae on the opposite margin.

Antenna (Fig. 2I): Endopod slightly longer than the exopod. The latter with 5 plumose setae as in the previous stage. An additional minute seta basally.

Mandible (Fig. 3C): Asymmetrical, slightly different in dentition. No palp at this stage.

Maxillule (Fig. 3I): Endopod with 1, 1, 3 setae. Basial endite unchanged. Coxal endite with 5 plumose and 1 fine setae.

Maxilla (Fig. 4C): Endopod with setation as 3 (rarely 2)+1+3. Scaphognathite with 8 marginal setae. The others unchanged.

Maxillipeds 1–3 (Fig. 5C, I, N): Setation unchanged. Endopod of maxilliped 3 longer than previous stage but not reaching the apical margin of basis.

Pereiopods (Fig. 7B): Rudimentary, unsegmented; pereiopod 1 chelate at tip. Pereiopods 2–3 as long as the cheliped.

Abdomen (Fig. 6C): A sixth segment is added; its posterior margin unarmed. Pleopods not present at this stage, but uniramous uropods emerging ventrally from the segment 6, each reaching approximately 2/3 of telson length. Uropod bifid apically, plus an additional inner spine subapically; distal inner border with 3 plumose setae.

Telson (Fig. 6C): Setation of 7+7 processes unchanged. Anal spine now absent.

*Fourth Zoea*

Dimension: CL=1.94–2.15 mm (mean 2.03 mm).

Carapace (Fig. 1D): Larger, but similar to the previous stages in general morphology.

Antennule (Fig. 2D): Peduncle indistinctly 3-segmented. Endopod unarmed distally. Outer

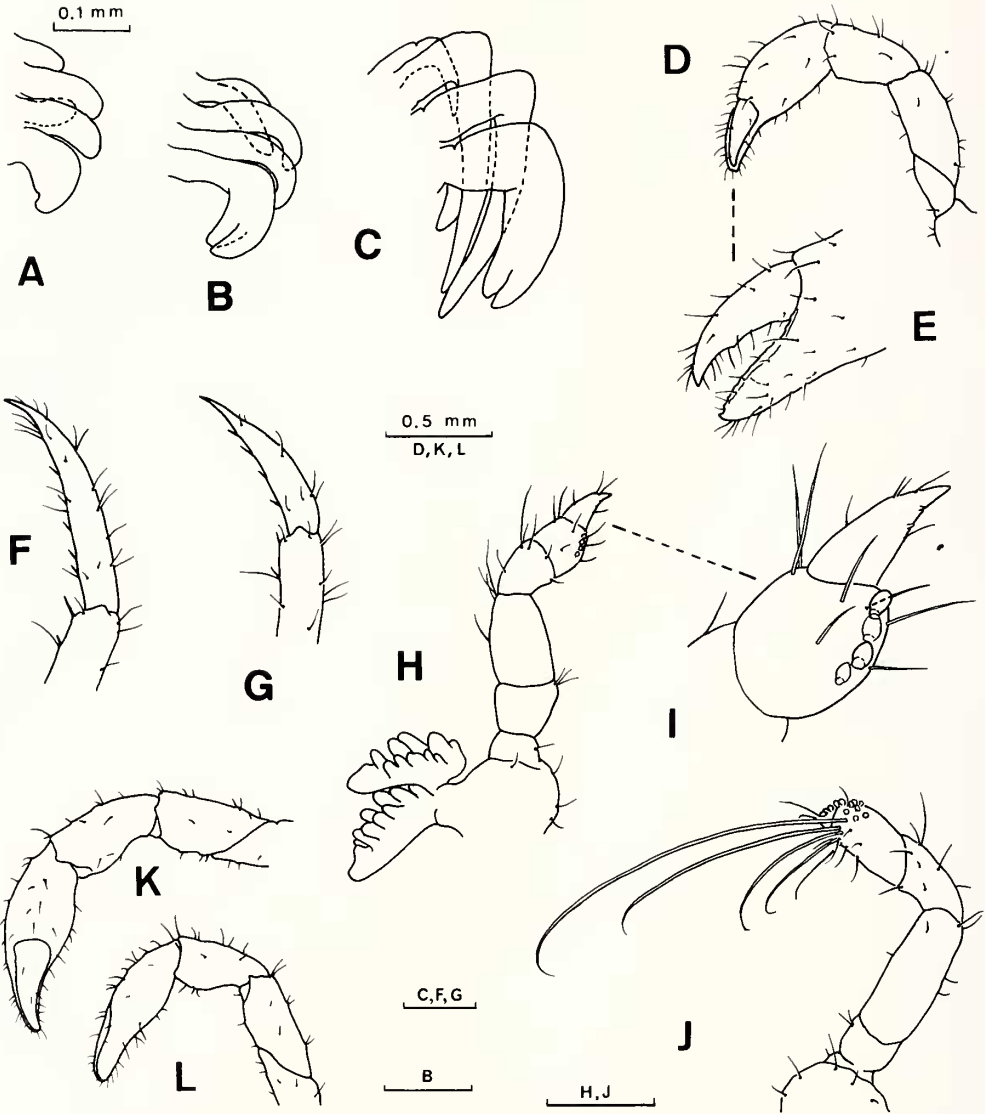


FIG. 7. *Pagurus middendorffii* Brandt, 1851. Pereiopods. A-C, rudiments of pereiopods of the zoea II-IV; D-J, pereiopods of the megalopa; D, right cheliped; E, detail of the chela; F-J, pereiopods 2-5, with a detail (I) of dactylus and propodus of the pereopod 4; K, L, right and left chelipeds of the first crab respectively. Scale bars=0.2 mm; others as indicated.

flagellum with 8 aesthetascs in total, arranged into three tufts.

Antenna (Fig. 2J): Endopod indistinctly segmented, more developed than the scale. Exopod with 5 setae on distal inner margin.

Mandible (Fig. 3D): Palp present as a soft unsegmented bud.

Maxillule (Fig. 3J): Basal endite with 6 stout spines and 2 inner setae. Coxal endite with 5 plumose and 2 simple setae.

Maxilla (Fig. 4D): Setations of endopod and basal endite unchanged. Proximal lobe of coxal endite with 5 setae; distal lobe with 4 or 5 setae. Scaphognathite with 13 plumose setae on margin,

projected posteriorly as a well-developed naked lobe.

Maxillipeds 1–2 (Fig. 5D, J): Both exopods with 8 plumose setae. The others unchanged.

Maxilliped 3 (Fig. 5O): Endopod well-developed, surpassing the basis in length, with 2 distal setae. Exopod with 8 natatory setae. Basis glabrous, as in the previous stages.

Pereiopods (Fig. 7C): Rudimentary, indistinctly segmented. Second and third pereiopods elongate, markedly longer than the cheliped.

Abdomen (Fig. 6D): With uniramous pleopods on segments 2–5; segment 6 with well-developed 2-segmented uropods. Endopod rudimentary, unarmed; exopod with 4 acute spines distally and 3 plumose setae on distal inner margin.

Telson (Fig. 6D): Setation as in the previous stage.

### *Megalopa*

Dimensions: CL=1.06–1.16 mm (mean 1.12 mm); CW=0.64 mm.

Carapace (Fig. 1E, e): Oblong, zoeal rostral spine reduced to a blunt rostrum. Surface sparsely covered with minute setae. Ocular peduncles each with a minute acicle on inner basal margin.

Antennule (Fig. 2E): Peduncle 3-segmented. Inner flagellum slender, 2-segmented, with 2 on proximal and 8 setae on distal segments. Outer flagellum 4-segmented, with 7, 4, 3 aesthetascs on segments 2–4. Distal segment markedly longer than the total length of the 3 proximal segments, with 4 distal setae, one of which is longer than the entire outer flagellum.

Antenna (Fig. 2K): Peduncle 4-segmented, distal segment elongate. Flagellum composed of 11 segments, each (except the first one) with short setae on distal margin; distal segment with 8 terminal setae. Acicle (=exopod) emerging laterally from the peduncle and armed with 4 setae.

Mandible (Fig. 3E): Palp greatly developed, indistinctly 3-segmented, with 3 minute setae distally. Mandibular plate strong, margin slightly rounded.

Maxillule (Fig. 3K): Greatly modified from the previous stages. Endopod digitiform, unsegmented, unarmed. Basal endite with 3 plumose setae and 11–12 minute smooth spines. Coxal

endite with 5 setae.

Maxilla (Fig. 4E): Endopod unsegmented, with a single apical seta. Basal endite with 9 on the proximal and 8 setae on the distal lobes. Coxal endite with 4 setae on each lobe. Scaphognathite greatly expanded, with 27 setae on margin.

Maxilliped 1 (Fig. 5E): Greatly modified from the previous stages. Endopod digitiform, unsegmented, unarmed, 1/2 exopod length. Exopod 2-segmented, with a short simple seta distally. Basal endite broad, with 14–15 short setae. Coxal endite with 3–4 setae.

Maxilliped 2 (Fig. 5K): Endopod 4-segmented, with 2 on the penultimate and 7 setae on the distal segments. Exopod 2-segmented, proximal segment greatly developed, glabrous; distal segment with 8 plumose setae.

Maxilliped 3 (Fig. 5P): Different from the maxillipeds 1–2; endopod markedly longer than exopod, 5-segmented; each segment with numerous setae, profusely setose on distal segments. Exopod 2-segmented, proximal segment with a single seta medially; distal segment with 7 setae.

Pereiopods (Fig. 7D–J): Well-developed, sparsely covered with short setae. Right cheliped larger than the left one; cutting borders of fingers hardened, lacking acute teeth. Pereiopods 2–3 cylindrical, long, similar in length, dactyli acutely pointed. Inner margin of dactylus of pereiopod 2 armed with 6 spinules and additional setae. Pereiopod 3 with 4 spinules and additional setae; propodi with 2 spinules on inner margin distally. Pereiopod 4 reduced, flattened distally; propodus with 4 spatuliform setae, dactylus triangular, with 2 spinules on inner border and additional setae. Pereiopod 5 reduced, subchelate, with 7–9 spatuliform setae on propodus and 3–4 on dactylus. Five long setae emerging from the propodus, of which the longest one is as long as the entire pereiopod.

Abdomen (Fig. 1E): Subcylindrical, slightly asymmetrical, sparsely covered with short setae, 6-segmented. Segments 2–5 each with a pair of well-developed pleopods; segment 6 with uropods. Pleopods (Fig. 6G, H) each with 2 distal hooked setae on endopod. Pleopods 1–3 with 9 long plumose setae on exopod. Pleopod 4 (=last) with 8 plumose setae.

Uropods (Fig. 6E): Left uropod slightly larger

than right one. Endopod with 3 "corneous granules" (better called *spatuliform seta*, see [7]) and 3 setae. Exopod well-developed, armed with 9–10 spatuliform setae on outer distal margin, 12 (left) or 10 (right) long plumose setae on margins, and 4 simple setae placed alternately among the plumose setae. Additional setae as illustrated.

Telson (Fig. 6E): Symmetrical, longer than broad, posterior margin rounded, with a mid-posterior group of 6 (occasionally 7) plumose setae, 2 minute setae located laterally, and short setae on surface.

#### *First Crab*

Dimensions: CL=1.10–1.20 mm (mean 1.16 mm); CW=0.73 mm (measured at mid portion).

Carapace (Fig. 1F): Elongate, lateral margins subparallel, surface smooth and with moderate transverse depression dorsally; front short. Ocular peduncles large, each with 1 spine basally.

Antennule (Fig. 2F): Inner flagellum 2-segmented, with 1 on proximal and 8 setae on distal segments. Outer flagellum now 5-segmented, with a total of 15 aesthetascs arranged into three tufts, proximal segment unarmed; apical segment without aesthetascs, but armed apically with 5 setae of which one is extremely long.

Antenna (Fig. 2L): Peduncle 4-segmented (fourth segment the longest); second segment with a well-developed acicle and a stout spine. Flagellum composed of 11 segments, each except the first armed with setae.

Mandible (Fig. 3F): Palp 3-segmented, distal segment ovoid, with 7 short setae on outer margin. Cutting edge almost straight.

Maxillule (Fig. 3L): Endopod unsegmented, with 2 setae laterally and additional 2 setae basally. Basal endite with 3 plumose setae and 14–15 smooth spines. Coxal endite ovoid, with 16–18 setae.

Maxilla (Fig. 4F): Endopod slender, with a single subapical seta. Basal endite bilobed, each lobe with 10–11 setae. Coxal endite bilobed, proximal lobe with 19–20 rigid curved setae arranged transversely and marginally, distal lobe with a total of 9 setae. Scaphognathite fringed with 26–28 plumose setae.

Maxilliped 1 (Fig. 5F): Endopod unsegment-

ed, digitiform, armed with 4 setae. Exopod 2-segmented, proximal segment with 3 plumose setae on outer margin and 2 simple setae on inner margin; distal segment with 6 plumose setae. Basis profusely setose, with a total of 20–21 setae arranged transversely and marginally. Coxa with 7–8 setae.

Maxillipeds 2–3 (not drawn): Similar in morphology to those of the megalopal stage, but profusely setose at this stage, especially the endopod of maxilliped 3; distal segments with numerous rigid setae and spines.

Pereiopods: Similar to those of the previous stage (see Fig. 1F). Chelipeds (Fig. 7K, L) markedly different in size, right larger than left, each covered with short setae.

Abdomen (Fig. 1F): Subcylindrical, segmentation indistinct, sparsely setose. Pleopods on abdominal segments 2–5, rather placed ventrolaterally. Left pleopods longer than right ones, each armed with plumose setae on exopod as illustrated; right pleopods with reduced, unarmed exopod. However, other specimens examined exhibited another range of pleopodal variation, i.e., first pair reduced to a very short bud-like projection, left pleopods 2–4 with 9, 9, 8 plumose setae on exopod, respectively, but right pleopods markedly reduced to buds.

Uropods (Fig. 6F): Left uropod larger than right one. Endopod with 6 (left) or 4 (right) spatuliform setae. Exopod with 12 (left) or 10 (right) spatuliform setae and additional setae on surface and margins.

Telson (Fig. 6F): Posterior margin divided into unequal lobes by a shallow sinus; surface and margins with several setae as illustrated.

### *Pagurus geminus* McLaughlin, 1976

#### *First Zoea*

Dimension: CL=1.09–1.15 mm (mean 1.13 mm).

Carapace (Fig. 8A, B): Surface smooth. Rostral spine slightly directed downward, not reaching the tip of antennal scale. Eyes sessile.

Antennule (Fig. 8C): Peduncle unsegmented, with 3 subequal aesthetascs and 2 fine setae



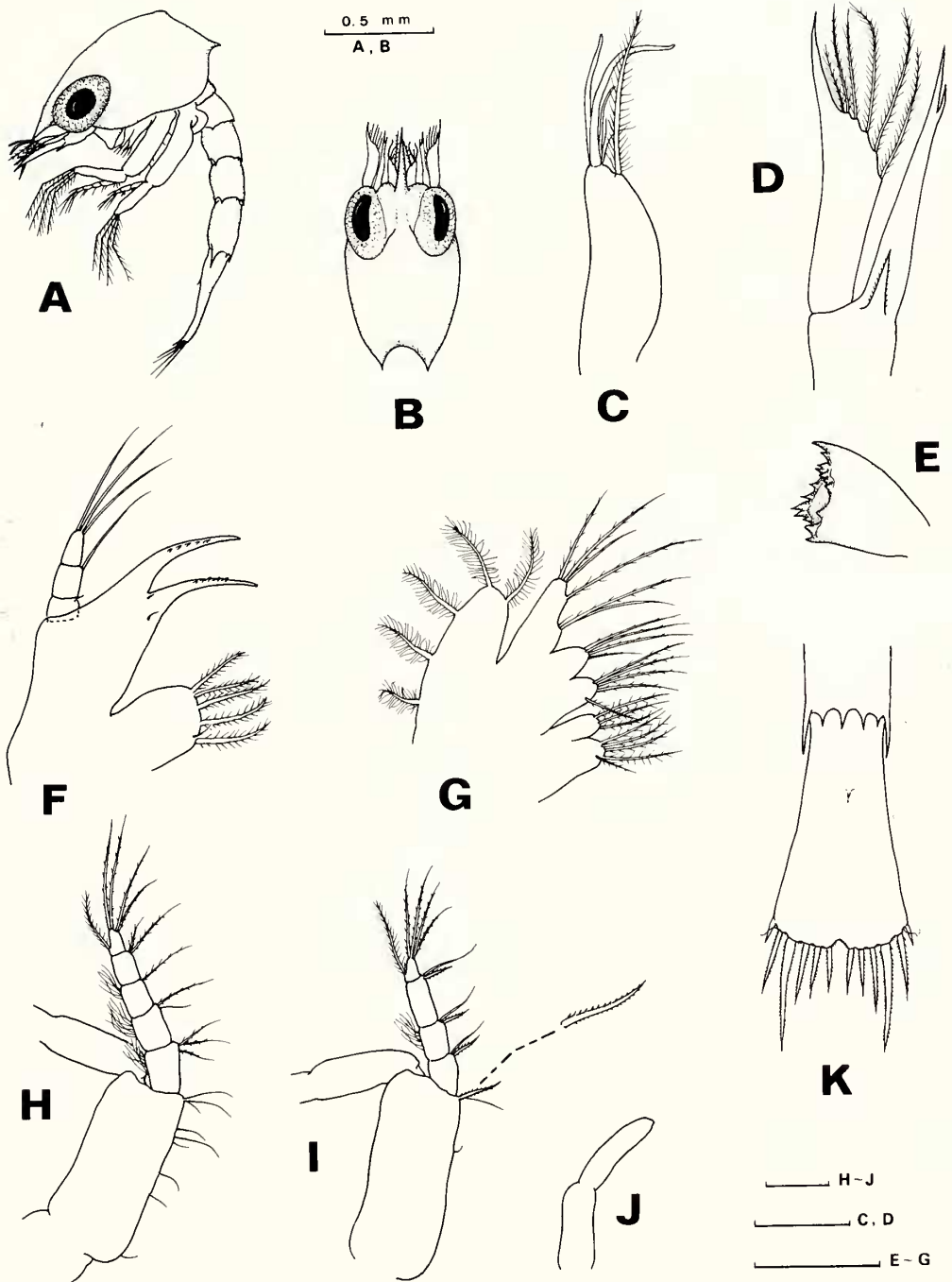


FIG. 8. *Pagurus geminus* McLaughlin, 1976. Zoea I. A, whole specimen, lateral view; B, carapace, antennules and antennae, dorsal view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H-J, maxillipeds 1-3; K, abdominal segment 5 and telson, dorsal view. Scale bars=0.1 mm, except for A and B.



distally, and subterminal, long plumose seta.

Antenna (Fig. 8D): Endopod bifid at tip, shorter than the exopod. Exopod distally pointed, with 6 plumose setae on inner distal half. A stout serrate spine near the base of endopod.

Mandible (Fig. 8E): Incisor process short, stout. Molar process with several acute teeth of diverse lengths.

Maxillule (Fig. 8F): Endopod 3-segmented, with 1, 1, 3 setae, the proximal a minute seta. Basial endite with 2 long curved stout spines and 2 minute inner setae. Coxal endite with 5 rigid plumose and 1 simple setae.

Maxilla (Fig. 8G): Endopod stepped medially, with 3+1+3 setae. Basial and coxal endites bilobed, with 5+4 and 5+3 setae respectively. Scaphognathite fringed with 5 soft plumose setae.

Maxilliped 1 (Fig. 8H): Endopod 5-segmented, setation as 3, 2, 1, 2, 4+I. Segments 1-3 with 6-7, 8, 5-7 very fine setules on outer margin respectively. Exopod with 4 long natatory setae. Basis with 9 setae along inner margin.

Maxilliped 2 (Fig. 8I): Endopod 4-segmented, setation as 2, 2, 2, 4+I. Segment 2 with 7-8 (rarely absent) fine setules dorsally. Exopod with 4 long, natatory setae. Basis with 3 setae marginaly, distal pair similar to setae of segments 1-3.

Maxilliped 3 (Fig. 8J): Rudimentary, uniramous, unarmed.

Pereiopods: Not observable at this stage.

Abdomen (Fig. 8K): Composed of 5 segments and a telson. Posterior margin of segments (except the first) with short spines. Posterolateral margins of fifth segment projected as stout spines.

Telson (Fig. 8K): Elongate, furcae apparent, each with 7 processes. Anal spine present medio-ventrally.

### *Pagurus lanuginosus* De Haan, 1849

#### First Zoea

Dimension: CL=1.53-1.59 mm (mean 1.57 mm).

Carapace (Fig. 9A): With a pointed rostral spine, slightly directed downward; posterolateral edges projecting moderately backward, distally acute.

Antennule (Fig. 9B): Peduncle unsegmented, distally invested with 3 aesthetascs, of which two are similar in length and one is short, slender, and 2 fine setae. Subterminally with 1 long plumose seta.

Antenna (Fig. 9C): Endopod slightly longer than the scale. Scale distally pointed, with 5 plumose setae on distal half of inner margin. A single stout serrate spine emerging from base of endopod.

Mandible (not drawn): Incisor process stout. Molar process with several pointed teeth of different lengths and minute granules on inner surface. Additional shorter teeth between both processes.

Maxillule (Fig. 9D): Endopod 3-segmented, with setae arranged as 2, 1, 3, of which the proximal ones are very short and fine. Basial endite with 2 long stout non-articulated spines and 2 fine setae. Coxal endite with 4-5 long and 2 shorter setae.

Maxilla (Fig. 9E): Endopod indistinctly bilobed, with 2 setae medially and 3-4 setae distally. Basial and coxal endites bilobed with 5+4 and 6+4 setae respectively. Scaphognathite fringed with 5 plumose setae.

Maxilliped 1 (Fig. 9F): Endopod 5-segmented, with setal arrangement as 3, 2, 1, 2, 4+I on inner margin; segments 1-3 with very fine long setules on outer margin arranged as 5-6, 10-11, and 9-10 respectively. Exopod with 4 long, plumose, natatory setae. Basis with 9 setae on inner margin.

Maxilliped 2 (Fig. 9G): Endopod 4-segmented, with 2 setae on segments 1-3, and 5 setae on distal segment of which one is dorsal. Segments 2-3 each with 4-5 and 5-6 very fine setules on outer margin respectively. Basis with 3 setae, the distal pair very similar to those of segments 1-3.

Maxilliped 3 (Fig. 9H): Rudimentary, uniramous, unarmed.

Pereiopods: No rudiments of pereiopods at this stage.

Abdomen (Fig. 9A, I): Composed of 5 segments and a telson. Posterior margin of each segment with minute spines; posterolateral spines of the fifth segment well-developed.

Telson (Fig. 9I): Elongate, approximately 1.5 times its posterior width, slightly notched medial-

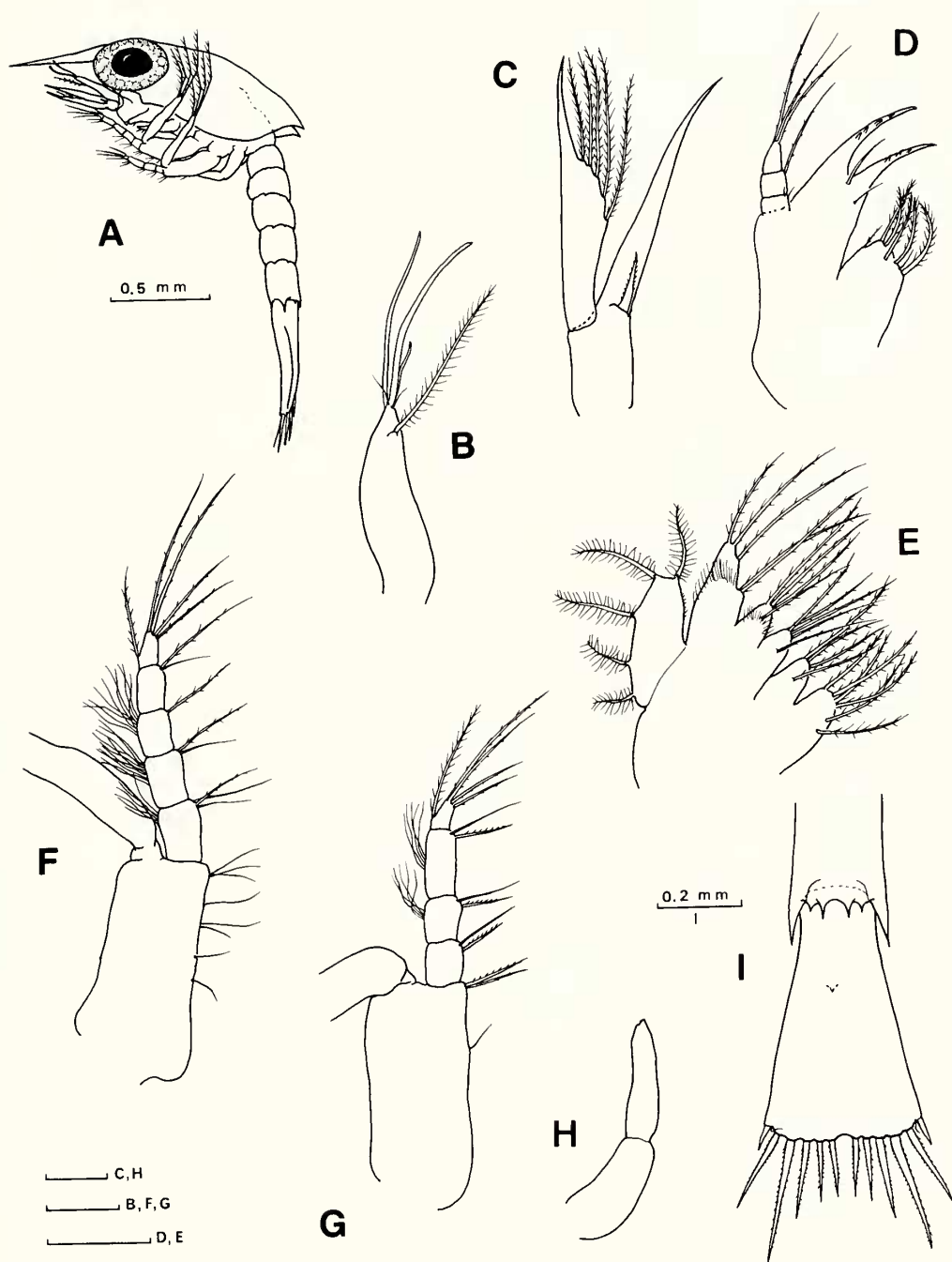


FIG. 9. *Pagurus lanuginosus* De Haan, 1894. Zoea I. A, whole specimen, lateral view; B, antennule; C, antenna; D, maxillule; E, maxilla; F-H, maxillipeds 1-3; I, abdominal segment 5 and telson, dorsal view. Scale bars = 0.1 mm, except for A and I.

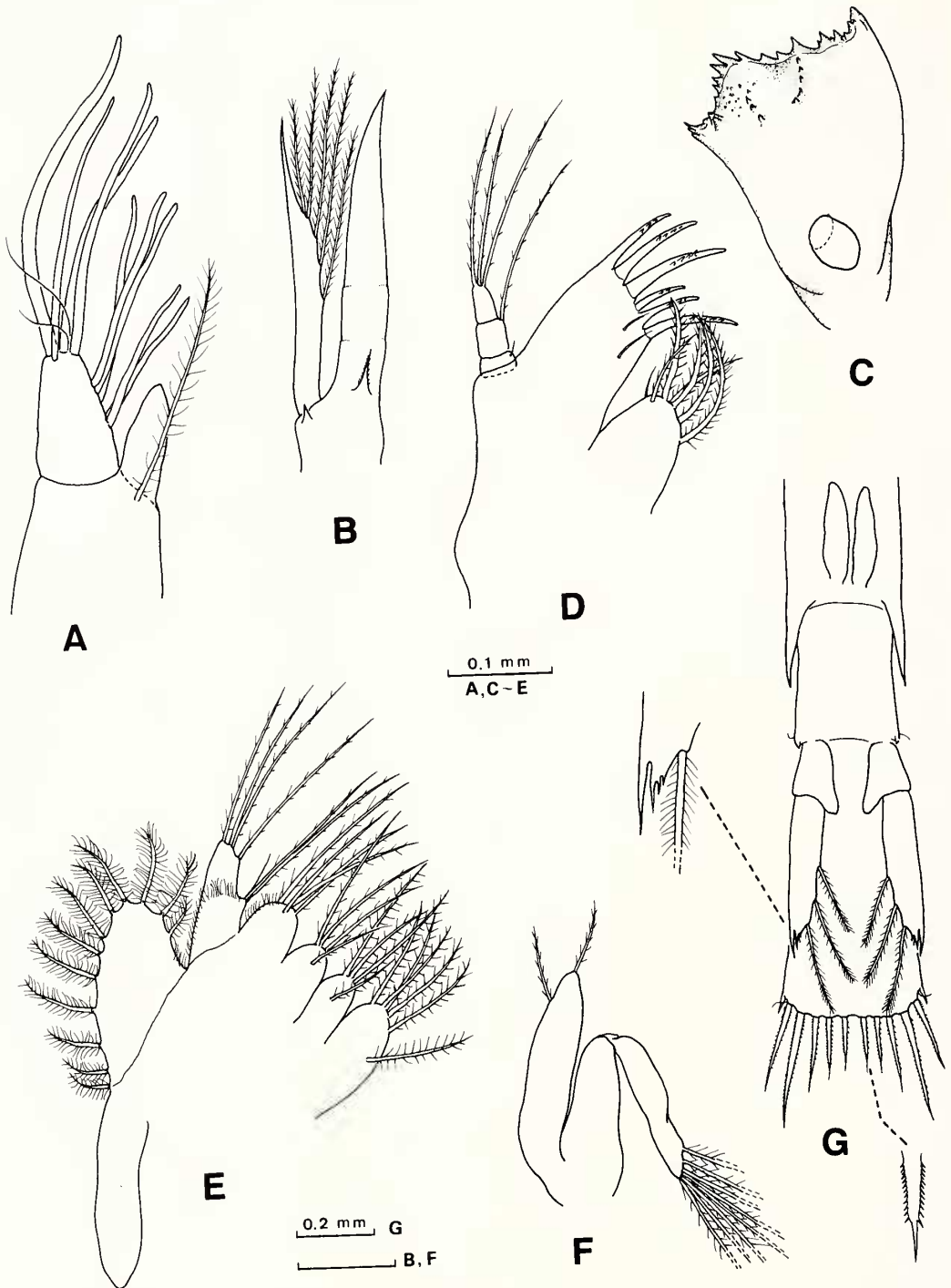


FIG. 10. *Pagurus lanuginosus* De Haan, 1849. Zoea IV. A, antennule (distal portion); B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped 3; G, last two abdominal segments and telson, ventral view, with details of distal portion of uropods and marginal seta. Scale as indicated.

ly. Posterior margin of each furca with 7 processes; outermost process a stout spine articulated to telson; second a fine seta (under high magnification it is seen as fringed with fine setules); third to seventh processes stout long setae (the fourth is the longest seta), each bearing setules along borders; processes 5–7 markedly pointed distally. Anal spine minute.

#### Fourth Zoea

Dimension: CL=1.90–2.12 mm (mean 2.03 mm).

Antennule (Fig. 10A): Endopod digitiform, unarmed. Outer flagellum indistinctly segmented, distally with 4 (rarely 3) aesthetascs and 2 fine setae, medially with 5 aesthetascs, arranged into two groups. A single, long plumose seta near base of endopod, and 2 fine setules on opposite margin. Segmentation distinct at level of endopod.

Antenna (Fig. 10B): Endopod thick, acute distally, slightly longer than scale. The latter with 5 plumose setae on inner margin. A stout serrate spine and a smaller smooth seta basally.

Mandible (Fig. 10C): Palp present as a soft unsegmented bud. Cutting border with several acute teeth.

Maxillule (Fig. 10D): Endopod 3-segmented, with 1, 1, 3 setae, the proximal seta very short and fine. Basal endite with 6 stout spines (some articulated at their bases) and 2 inner simple setae. Coxal endite with 6 rigid plumose and 1 simple setae.

Maxilla (Fig. 10E): Endopod stepped medially, with 3+1+3 setae. Basal and coxal endites bilobed, with 5+4 and 6+4 setae respectively. Scaphognathite composed of distal and proximal lobes, the former with 11–12 soft plumose setae and the latter unarmed.

Maxillipeds 1–2: Not dissected.

Maxilliped 3 (Fig. 10F): Endopod greatly developed, longer than protopod, with 1 terminal and 1 subterminal setae. Exopod 2-segmented, distal segment with 8 long natatory setae.

Abdomen (Fig. 10G): Composed of 6 segments and the telson. Uniramous, unarmed paired pleopods on abdominal segments 2–5; segment 6 with well-developed 2-segmented uropods. Endopod as a short unarmed projection. Exopod

elongate, with 4 pointed spines distally and 3 plumose setae on inner distal half.

Telson (Fig. 10G): Elongate, posterior margin almost straight, with 7 processes on each furca; processes 5–7 markedly acute distally. Anal spine absent.

## DISCUSSION

Kurata [3] described the zoea I stage of *P. middendorffii* from laboratory-reared larvae, and assigned a series of planktonic zoeas II–IV to the same species. Morphological comparison of all zoeal stages between Kurata's and our study is shown in Table 1.

The larval characters of the zoea I stage are almost identical in both studies, whereas Kurata's zoeas II–IV of *P. middendorffii* are different from those of our entirely laboratory-reared material, e.g., even in important characters such as the maxillary scaphognathite and telsonal processes. This fact suggests that the specific identification was inadequate in his planktonic material. What species shall we attribute these planktonic zoeas to? Up to present, as shown in Table 2, the complete larval developments of 9 pagurid species from Japan except *P. trigonocheirus* have been described from laboratory-rearing which insures correct specific identification. Among them, zoeas of the following 4 species have 8+8 telsonal setation in the stages II–IV, as well as 3 setae on exopod of uropods in the III–IV stages: *P. brachiomastus*, *P. hirsutiusculus*, *P. dubius* and *P. geminus*. However, no zoea IV of these species has 14 marginal setae on the maxillary scaphognathite as in Kurata's material [3]. Larvae of the other allied species from Hokkaido, such as *P. ochotensis* [7] and *P. lanuginosus* (this study), are quite different from those of Kurata's "*middendorffii*", especially in the setations of antenna (exopod), maxilla (coxal endite), uropods (exopod), along with the marginal setation of the telson.

Other *Pagurus* species occurring in the coasts of Hokkaido [1, 2] are *P. hirsutiusculus* (Dana, 1851), *P. constans* (Stimpson, 1858), *P. gracilipes* (Stimpson, 1858), *P. pectinatus* (Stimpson, 1858), *P. trigonocheirus* (Stimpson, 1858), *P. dubius*

TABLE 1. Comparison of zoal characters of *Pagurus middendorffii* between Kurata's [3] material and this study [\*]

| Characters          | Zoea I    |         | Zoea II   |         | Zoea III  |           | Zoea IV   |         |
|---------------------|-----------|---------|-----------|---------|-----------|-----------|-----------|---------|
|                     | Kurata    | *       | Kurata    | *       | Kurata    | *         | Kurata    | *       |
| Source of Material: | L         | L       | P         | L       | P         | L         | P         | L       |
| Carapace:           |           |         |           |         |           |           |           |         |
| length (mean; mm)   | 1.24      | 1.34    | 1.75      | 1.51    | 2.16      | 1.82      | 2.50      | 2.03    |
| Antennule:          |           |         |           |         |           |           |           |         |
| aesthetascs         | [2]**     | 2       | 2         | 3       | 4         | 5         | 9         | 8       |
| endopod bud         | [-]       | -       | -         | -       | +         | +         | +         | +       |
| endopod seta        | [(1)]     | (1)     | (1)       | (1)     | 1         | 1         | -         | -       |
| Antenna:            |           |         |           |         |           |           |           |         |
| exopod setae        | 6         | 6       | 6         | 5       | 6         | 5         | 6         | 5       |
| Mandible:           |           |         |           |         |           |           |           |         |
| bud of palp         | -         | -       | -         | -       | -         | -         | +         | +       |
| Maxillule:          |           |         |           |         |           |           |           |         |
| coxal endite        | [5]       | 7       | [6]       | 7       | [7]       | 6         | [7]       | 7       |
| basial endite       | [2sp+1]   | 2sp+2   | [4sp+1]   | 4sp+2   | [4sp+1]   | 4sp+2     | [6sp+1]   | 6sp+2   |
| endopod             | [1, 1, 3] | 1, 1, 3 | [1, 1, 3] | 2, 1, 3 | [1, 1, 3] | 1, 1, 3   | [1, 1, 3] | 1, 1, 3 |
| Maxilla:            |           |         |           |         |           |           |           |         |
| coxal endite        | [4+3]     | 5+4     | [5+4]     | 5+4     | [5+4]     | 5+4       | [5+4]     | 5+4 (5) |
| basial endite       | [3+3]     | 5+4     | [4+4]     | 5+4     | [5+4]     | 5+4       | [5+4]     | 5+4     |
| endopod             | [2+1+3]   | 2+1+3   | [3+1+3]   | 3+1+3   | [3+1+3]   | 3 (2)+1+3 | [3+1+3]   | 3+1+3   |
| scaphognathite      | [5]       | 5       | [6]       | 6       | [10]      | 8         | [14]      | 13      |
| Mxp. 1, endopod:    |           |         |           |         |           |           |           |         |
| segment 1           | [3+n]     | 3+n     | [3+I]     | 3+I     | ?         | 3+I       | ?         | 3+I     |
| segment 2           | [2+n]     | 2+n     | [2+I]     | 2+I     | ?         | 2+I       | ?         | 2+I     |
| segment 3           | [1+n]     | 1+n     | [1+I]     | 1+I     | ?         | 1+I       | ?         | 1+I     |
| segment 4           | [2]       | 2       | [2]       | 2       | ?         | 2         | ?         | 2       |
| segment 5           | [4+I]     | 4+I     | [4+I]     | 4+I     | ?         | 4+I       | ?         | 4+I     |
| Mxp. 2, endopod:    |           |         |           |         |           |           |           |         |
| segment 1           | [2]       | 2       | [2]       | 2       | ?         | 2         | ?         | 2       |
| segment 2           | [2+n]     | 2+n     | [2+I]     | 2+I     | ?         | 2+I       | ?         | 2+I     |
| segment 3           | [2+n]     | 2+n     | [2+I]     | 2+I     | ?         | 2+I       | ?         | 2+I     |
| segment 4           | [4+I]     | 4+I     | [4+I]     | 4 (3)+I | ?         | 4+I       | ?         | 4+I     |
| Mxp. 3:             |           |         |           |         |           |           |           |         |
| endopod setae       | -         | -       | 1         | 1       | ?         | 1         | ?         | 2       |
| Abdomen:            |           |         |           |         |           |           |           |         |
| pleopod             | -         | -       | -         | -       | -         | -         | +         | +       |
| uropod setae        | -         | -       | -         | -       | 3         | 3         | 3         | 3       |
| Telson:             |           |         |           |         |           |           |           |         |
| processes           | 7+7       | 7+7     | 8+8       | 7+7     | 8+8       | 7+7       | 8+8       | 7+7     |

\*\* Data in brackets are estimated from illustrations. n: numerous, sp: spine, I: dorsal plumose seta, L: laboratory-reared, P: plankton, +: present, -: absent, ?: no data.

(Ortmann, 1892), and *P. rathbuni* (Benedict, 1892). But larval studies, except those of *P. hirsutiusculus* (see [9]), *P. dubius* (see [10]) and *P. trigonocheirus* (see [7, 11]) are unknown to refer to.

In the present study, there were conspicuous differences between the larvae of *P. geminus* and the other two species. The bifid character of

antennal endopod clearly distinguishes *P. geminus* from the other allied species [6]. Thus, two possibilities are suggested by the facts mentioned above: 1) Kurata's zoeas II-IV belong to another species whose larvae are unknown, 2) each zoal stage of these planktonic larvae also may be assigned to different species, although this probability is more difficult to ascertain. At present, we



TABLE 2. Comparison of selected zoeal characters and their setation in known pagurid species from Japan

| Species                  | Antenna (Z I) |         | Maxillule (Z I) | Maxilla     |             | Uropod (Z III-IV) |       | Telson (Z II-IV) | Ref.    |
|--------------------------|---------------|---------|-----------------|-------------|-------------|-------------------|-------|------------------|---------|
|                          | exo.          | endo.   | endo.           | (Z I) endo. | (Z IV) sca. | exo.              | endo. | processes        |         |
| <i>Pagurus</i>           |               |         |                 |             |             |                   |       |                  |         |
| <i>lanuginosus</i>       | 5             | simple  | 1, 1, 3         | 3+1+3       | 12          | 3                 | +     | 7+7              | [5, *]  |
| <i>middendorffii</i>     | 6             | simple  | 1, 1, 3         | 2+1+3       | 13          | 3                 | +     | 7+7              | [*]     |
| " <i>middendorffii</i> " | 6             | simple  | 1, 1, 3         | 2+1+3       | 14          | 3                 | +     | 8+8              | [3]     |
| <i>brachiomastus</i>     | 6             | simple  | 1, 1, 3         | 3+1+3       | 12          | 3                 | +     | 8+8              | [6]     |
| <i>hirsutiusculus</i>    | 5             | simple  | 0, 1, 3         | 3+1+3       | 12          | 3                 | +     | 8+8              | [9]     |
| <i>ochotensis</i>        | 7             | simple  | 2, 1, 3         | 3+1+3       | 15-16       | 4-5               | +     | 8+8              | [7]     |
| <i>dubius</i>            | 5             | bifid   | 0, 1, 3         | 2+1+3       | 11          | 3                 | +     | 8+8              | [10]    |
| <i>geminus</i>           | 6             | bifid   | 1, 1, 3         | 3+1+3       | ?           | 3                 | +     | 8+8              | [4, *]  |
| <i>trigonocheirus</i>    | 8             | bifid   | 1, 1, 3         | 3+1+3       | ?           | ?                 | ?     | ?                | [7, 11] |
| <i>similis</i>           | 10            | 2 setae | 1, 1, 3         | 3+3         | 11          | 7                 | 2     | 8+8              | [12]    |
| <i>Labidochirus</i>      |               |         |                 |             |             |                   |       |                  |         |
| <i>splendescens</i>      | 7             | simple  | 1, 1, 3         | 3+1+3       | 17-18       | 7-8               | 0-1   | 8+8              | [13]    |

endo.: endopod, exo.: exopod, sca.: scaphognathite, Z: zoea, Ref.: references, +: present, ?: no data, \* this study.

have no complete larval information concerning about 40% of the Paguridae from Hokkaido. Future larval studies will answer the above cited question.

Most of pagurid zoeas exhibit 7 processes on each telsonal furca in the zoea I stage and a setation of 8+8 in the zoea II-IV stages. This led to generalize that all pagurid zoeal stages II-IV exhibit this setation [3, 13]. However, the first record of setation of 7+7 processes throughout zoeal stages was given for *P. lanuginosus* [5]; this setation is also consistent with our material (see Fig. 10G). The present descriptions of *P. middendorffii* also indicate that the previous presumption is not applicable to all known *Pagurus* zoeas.

An anal spine is present in only the zoeal stages I and II in most of known pagurid larvae. Additional specimens of zoea I stage of *P. brachiomastus* and *P. ochotensis*, although previously described [6, 7] were reexamined. The anal spine was minute and short in *P. geminus* and *P. lanuginosus*, moderate in *P. middendorffii*, but conspicuous in *P. brachiomastus* and *P. ochotensis*.

Besides the telsonal setation of 7+7, the zoeal stages II-IV of *P. middendorffii* and *P. lanuginosus* have characters common to both species. A

number of megalopal characters, especially the 6 telsonal plumose setae is shared by these species and also by *P. hirsutiusculus* [9]. Most of megalopas known from Japan exhibit 8 marginal setae [6].

Kurata [3] briefly described and distinguished 5 types of *Pagurus* megalopas by the length of antennal scale, cheliped ornamentation, rostrum length, and proportion of dactylus to propodus of pereopods II-III. It is now known that at least one of *Pagurus* megalopas belongs to a different genus, *Paguristes* [7], but the correct assignment of the remaining megalopas is still uncertain because of his brief descriptions and incomplete illustrations.

The present material of *P. lanuginosus* from Hokkaido differs in a few minor features from the larvae of the same species from Korea reported by Hong [5]. However, the most conspicuous difference is the presence of mandibular palp in all specimens of zoea IV from Hokkaido (see Fig. 10C), not observed by Hong. This palp is rather located basally, so it seems likely that Hong was probably unaware of its nature (his illustrations rather emphasized the dentition). It seems that the other minor differences can occur due to the extensive geographical range and different habitats

in which the adults and planktonic larvae of this species inhabit, i.e. Pacific coast, Hokkaido, and Pusan, Korea, including different laboratory conditions used. The first megalopas of *P. lanuginosus* were obtained after 21 days of culture, whereas in the Hong's study, these appeared after 31–32 days. Under the laboratory conditions of 18°C temperature and 31.5 ppt salinity, the duration of each zoeal stage was approximately 5–6 days in our study and 7–9 days in Hong's study (at 13.6°C and 33.67 ppt).

Although zoeas and megalopas of *P. lanuginosus* and *P. middendorffii*, sympatric species in the sublittoral of Hokkaido have a number of similar characters ([5], this study), the adults are so distinct that their larval resemblance may suggest some phylogenetic significance. In fact, adults of *P. lanuginosus* have hairy pereopods with scattered brownish spots ([15], our material), whereas those of *P. middendorffii* are smooth, without coloured spots ([16], our material).

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